Survival of *Archytas marmoratus* (Diptera: Tachinidae) from Superparasitized Corn Earworm Larvae (Lepidoptera: Noctuidae)

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ABSTRACT   We investigated the survival of *Archytas marmoratus* (Townsend) from superparasitized *Helicoverpa zea* (Boddie) larvae. About half of the planidia of *A. marmoratus* brushed on larvae of the corn earworm, *H. zea*, became established. Fourth instars were more susceptible to parasitization than other instars, but parasitoid eclosion from superparasitized hosts was greatest in fifth instars. The number of hosts producing *A. marmoratus* adults declined linearly with the number of maggots per host, with no eclosion of *A. marmoratus* from hosts with >10 maggots. When third-instar corn earworm were collected from artificially infested, whorl-stage corn after the release of *A. marmoratus*, 75% of the parasitized larvae were superparasitized. Superparasitism reduced parasitoid eclosion more severely in field plots than in the laboratory. As in laboratory studies, the number of hosts producing *A. marmoratus* adults declined linearly with an increased number of maggots, but no parasitoid eclosed if hosts had more than four maggots. The number of maggots per corn earworm larva was highly correlated with percentage parasitism. Consequently, the release rate of *A. marmoratus* might need to be adjusted to host density so that superparasitism does not reduce the survival rate of the parasitoid.

KEY WORDS   *Archytas marmoratus, Helicoverpa zea*, biological control, Tachinidae, augmentation, inundative release

Archytas marmoratus (TOWNSEND) is a solitary, larval-pupal parasitoid indigenous to the southern United States, Central America, the West Indies, and South America as far south as Chile (Sabrosky 1955). In Georgia, *A. marmoratus* is generally a late-season parasitoid of several noctuid species, including the corn earworm, *Helicoverpa zea* (Boddie). Although early-season populations of *A. marmoratus* are inadequate to prevent damage by the corn earworm, researchers have suggested a role for this parasitoid in area-wide management through augmentation (Gross and Young 1984; Gross 1988, 1990; Knipling 1992). Up to 40,000 parasitoids have been produced weekly (Gross and Johnson 1985, Bratti and Costantini 1991, Gross 1994, Gross et al. 1996) and mass production is technically feasible. After inundative releases of *A. marmoratus* in whorl-stage corn, parasitism of the corn earworm increases several fold (Proshold et al. 1998).

Knipling (1992) stated that progeny of the released parasites are more important than the released parasites in managing pest populations by augmentation of natural enemies. For *A. marmoratus,* superparasitism can prevent eclosion of parasitoids and population build-up in field cages (Gross and Young 1984), and only one parasitoid will eclose from superparasitized hosts (Reitz 1995). In the last year of a 3-yr pilot test

(Proshold et al. 1998), 70% of the parasitized corn earworm larvae collected from release fields was superparasitized. No parasitoid eclosed from hosts with more than four maggots (32% of parasitized hosts). Eclosion from hosts with three or four maggots was half the eclosion from hosts with less than three maggots.

The objective of this study was to determine the relationship between superparasitism of the corn earworm and eclosion of *A. marmoratus.*

Materials and Methods

Insects. *A. marmoratus* has been maintained in a laboratory colony since 1981 with intermittent infusion of feral individuals from parasitized larvae of the corn earworm and fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), collected from whorl-stage corn in Georgia and Florida. The *A. marmoratus* colony has been maintained on corn earworm from the Tifton, GA, laboratory colony (Young et al. 1976) according to the methods of Gross and Johnson (1985). Corn earworm larvae were reared on corn-soy-meal (CSM) artificial diet (Jones et al. 1977) according to the methods of Burton (1969). Corn earworm larvae used to infest whorl-stage corn were progeny of irradiated (100 Gy) male moths crossed with nonirradiated female moths. These corn earworm larvae would produce sterile adults if they escaped parasitism and were not collected (Carpenter et al. 1987). Both test and colony

insects were reared at 25°C and a photoperiod of 12:12 (L:D) h. For clarity we refer to newly hatched *A. marmoratus* as planidia, and parasitoids that have entered host larvae as maggots.

Laboratory Studies. *Experiment 1.* Planidia were extracted mechanically as described by Gross and Johnson (1985) and dropped on the inner surface of diet-cup lids. The number of planidia per lid was adjusted to 10, 20, or 30 and placed in cups containing *H. zea* larvae. Each treatment (10, 20, or 30 planidia per lid) included 20 host larvae of each of four developmental stages (third, fourth, early-fifth, or late-fifth instars). We held insects until death or eclosion of host or parasitoid, and we recorded the number of maggots observed beneath the pupal integument and within dead larvae, the host pupation date, and the date of the parasitoid or host eclosion.

Experiment 2. In the first trial, planidia were placed on host larvae (third, fourth, early-fifth, or late-fifth instar) with a brush (1, 3, 6, or 9 planidia per larva, *n* = 15 larvae per treatment per instar). In addition, groups of 10 late-fifth instars received 12, 15, or 18 planidia. In a second trial, each treatment included 3, 6, 9, or 12 planidia on third, fourth, early-fifth, or late-fifth instar corn earworm (*n* = 25). In addition, two groups of 25 late-fifth instars received 15 or 18 planidia. Data were recorded as in experiment 1.

Field Studies. Ten fields (0.7–9.0 ha) were selected in Tift or Berrien County, GA. Four of the fields were surrounded by woodland and another three were surrounded by woodland on three sides. Harper-1 and Harper-2 were adjacent and separated by a row of trees. All other fields were isolated from other corn. Third-instar progeny from corn earworm females crossed with irradiated males (100 Gy) were placed in the inner whorl of corn during the whorl stage. In one field (Stone), 75 larvae were placed in each of two rows 10 rows apart on the south side of the field. Three larvae were placed at a site, one larva in each of three consecutive corn plants, 25 sites per row. Each site was ≈5 m apart. In the other nine study fields, 60 whorls were infested with a larva in each corner of the field. The larvae were set out in two transects per corner, 10 sites per transect (≈5 m apart). Three larvae were placed per site as previously described for a total 240 larvae per field. All 10 fields were infested on the same day.

Archytas marmoratus was reared by the method of Gross (1994) with modifications as described by Proshold et al. (1998). After female flies emerged, they were allowed to mature for the requisite 10–12 d prelarviposition period before release. Release boxes containing adult parasitoids were uniformly distributed in each field. Studies by Gross (1990) indicated that release rates of ≈370 and 860 female *A. marmoratus* per hectare would yield ≈50 and 80% parasitism of late-instar corn earworm larvae, respectively. During 17 wk in 1995, weekly production of females was 190 ± 6.4 (average ± SEM) per box with 86 ± 1.0% mating (unpublished data). Based on these observations, the number of boxes placed per field varied depending on the size of a field so that the number of *A. marmoratus* would range from 200 to 1,000 females per hectare. Adults in four randomly selected boxes from each week's production were counted after a release to estimate the number per box. Twenty-five females from each box were dissected for the presence of planidia to verify that all females had mated and that the planidia were mature enough for larviposition.

Female *A. marmoratus* locate larviposition sites using kairomones associated with frass of their host (Nettles and Burks 1975). Because of this we set out boxes 4 to 6 d after corn whorls were artificially infested so that F_1 host larvae would have fed and produced frass. F_1 larvae were collected 7–9 d after infestation (3 d after *A. marmoratus* females were released). At that time, study fields were surveyed for feral larvae and all corn earworm and fall armyworm larvae sampled were collected to determine percentage parasitism (Proshold et al. 1997).

Data Analysis. Frequency data were analyzed for homogeneity with a log-likelihood-ratio test (Sokal and Rohlf 1969). Data were pooled so that cell frequencies were ≥5. If cell frequencies were <5 after pooling, data were analyzed by Fisher two-tailed, Exact Test (PROC FREQ, SAS Institute 1989). Data on the number of maggots per corn earworm larva, percentage parasitism, number of released females per hectare, and number of maggots per larva were tested for normality using the Kolmogorov–Smirnov statistic (PROC UNIVARIATE, SAS Institute 1989). Data that were normally distributed, or could be normalized using the arcsine transformation were subjected to an analysis of variance (ANOVA), linear or polynomial regression (PROC GLM, SAS Institute 1989). Data that could not be normalized were subjected to a nonparametric ANOVA (PROC NPAR1WAY, SAS Institute 1989).

Results

Laboratory Studies. *Experiment 1.* For the 10-planidia treatment, 91% of the corn earworm larvae (75–100%, depending on instar treated) were parasitized and 85% (60–95%) were superparasitized. As the number of planidia increased, superparasitism increased and the distribution of number of maggots per parasitized corn earworm became more variable (Fig. 1). Fewer larvae became parasitized when treated as third instars than when treated as fourth or fifth instars. Even with 30 planidia, two third instars (10%) were not parasitized. The maximum number of maggots within a host was 25 (the host pupated but no parasitoid eclosed).

Parasitoid survival decreased with an increase in the number of planidia per treatment. For the 10-planidia treatment, a parasitoid eclosed from about half of the parasitized corn earworm larvae and only one parasitized host failed to pupate. For the 20- and 30-planidia treatments, fly eclosion decreased and host mortality increased. For these two treatments, only 29 and 11% of the parasitized corn earworm larvae produced adult parasitoids, respectively. No parasitoid eclosed from a host with >10 maggots (Fig. 2). A
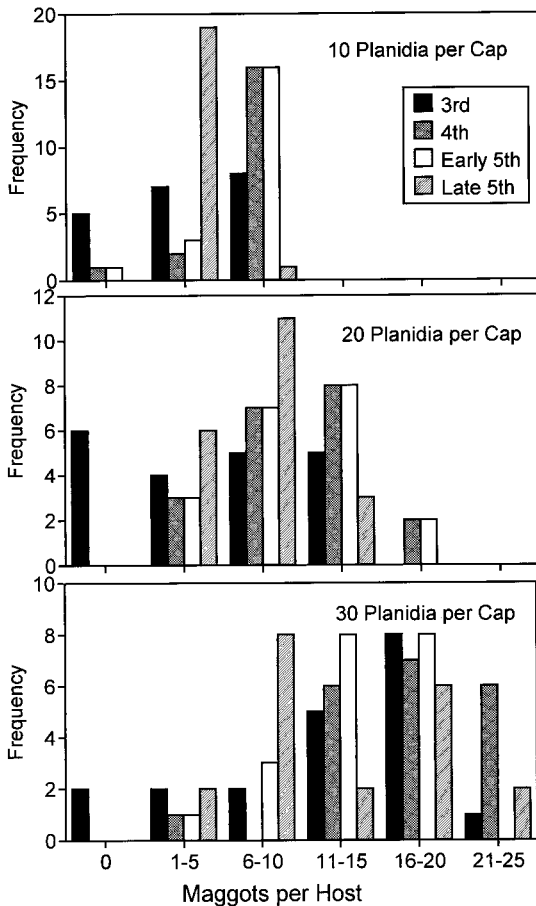
Fig. 1. Frequency distribution of number of maggots per corn earworm when 10, 20, or 30 planidia were placed on the lid of diet containers holding third, fourth, early-fifth, or late-fifth instars.

greater proportion of the corn earworm larvae that died had more maggots than did the corn earworm pupae that died ($G = 7.646$, df $= 2$, $P = 0.022$). Thus, with an increase in the number of planidia, superpar-
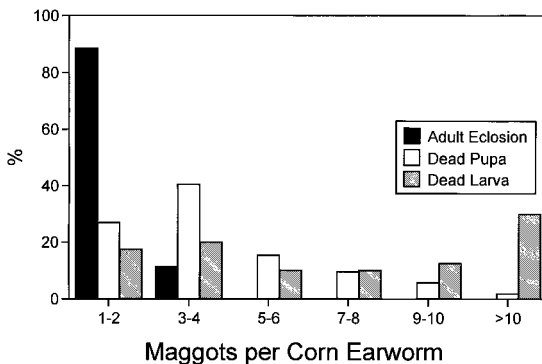

Fig. 2. Fate of parasitized corn earworm larva or parasitoid with an increase in the number of maggots per host.
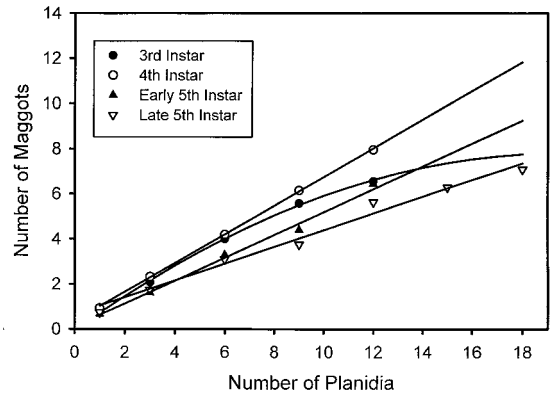

Fig. 3. Number of maggots within corn earworm larvae as a function of the number of *A. marmoratus* planidia placed on third ($y = 0.800x - 0.0203x^2 - 0.0578$), fourth ($y = 0.636x + 0.389$), early-fifth ($y = 0.507x + 0.119$), or late-fifth instars ($y = 0.371x + 0.679$).

asitism increased and eclosion of adult parasitoids decreased.

Tests 3 and 4. Maggot infestation per host was directly related to the number of planidia placed on larvae for corn earworm treated during the fourth and fifth instars (Fig. 3) (data from tests 3 and 4 combined). Planidia were more successful in parasitizing fourth than fifth instars of the corn earworm. The number of maggots per corn earworm treated as late-fifth instars was nearly as great as the number from treated early-fifth instars, but late-fifth instars with 18 planidia contained fewer maggots than fourth instars with 12 planidia. The number of maggots infesting third instars as function of number of planidia increased curvilinearly, leveling off at about seven maggots per larva.

Nonparasitized corn earworm larvae emerged as adults 11.4 ± 0.20 d after pupation ($n = 18$), several days less than the development time of *A. marmoratus*. Female parasitoids required about one more day for eclosion than males ($F = 135.8$; df $= 1, 478$; $P < 0.001$; average $= 17.0 \pm 0.064$ and 16.0 ± 0.060 d, respectively). There was a significant curvilinear relationship between days to eclosion for *A. marmoratus* and age of host larva when parasitized (Fig. 4). *A. marmoratus* from corn earworm larvae that pupated 3 d after treatment with planidia (late-fifth instar) eclosed 18.7 (females) and 17.1 (males) d after host pupation; however, those from larvae pupating 9 d after treatment (third instar) eclosed 16.1 (females) and 15.5 (males) d after host pupation. Developmental time from host pupation to eclosion was similar for *A. marmoratus* from corn earworm larvae treated as third, fourth, or early-fifth instars.

As with the previous test, we observed no eclosion of *A. marmoratus* if corn earworm pupae contained >10 maggots. When corn earworm larvae were parasitized as third, fourth, or early-fifth instars, we observed an inverse relationship between parasitoid eclosion and the number of maggots per host, with no
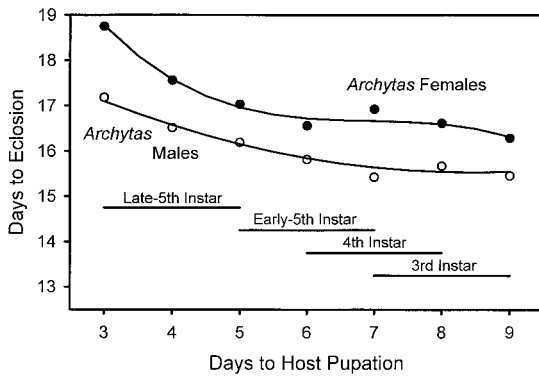
Fig. 4. Number of days from host pupation to eclosion for *A. marmoratus* ♀♀ (y = 27.723 − 4.717x + 0.672x² − 0.0324x³) and ♂♂ (y = 19.310 − 0.897x + 0.0531x²) as a function of days to host pupation when planidia were placed on third, fourth, or fifth-instar corn earworm.

significant difference because of host-stage treated (F = 2.18; df = 2, 27; P = 0.132, data for tests 2–4 combined). For third through early-fifth instars, percentage survival of *A. marmoratus* from parasitized corn earworm declined by ≈9% for each additional maggot (Fig. 5). Eclosion of *A. marmoratus* declined curvilinearly with number of maggots per host parasitized as late-fifth instars. However, for up to nine maggots, survival declined linearly at a rate of ≈3% for each additional maggot. Only 13% of the corn earworm larvae superparasitized with 10 maggots produced adult parasitoids.

Field Studies. Five hundred (22%, range from 4 to 35%) of the F_1 larvae placed in whorl-stage corn were recovered (Table 1). Of those, 23% were parasitized and 18% were superparasitized. Ninety-three feral corn earworm larvae (from five fields) and 194 fall armyworm larvae (from six fields) were collected. Nearly 10% of feral larvae of the corn earworm were parasitized and 5% superparasitized. Only two of the fall armyworm larvae were parasitized with one maggot each. When summed over fields with feral corn earworm larvae, significantly fewer feral than F_1 larvae were parasitized (G = 12.932, df = 1, P = 0.001). However, on a field-by-field basis, significant probabilities were not obtained. Fisher probability was 0.063 for the Houston location and >0.3 for
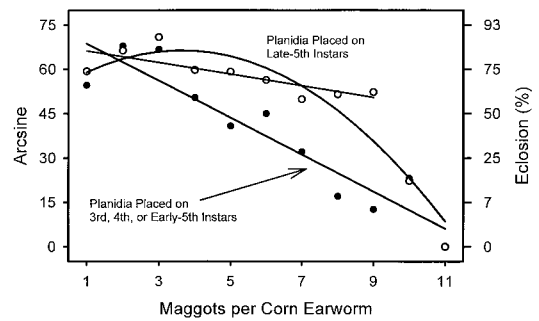

Fig. 5. Percentage eclosion [arcsine$\sqrt{(\%/100)}$ and back transformation] of *A. marmoratus* as a function of the number of maggots per parasitized corn earworm when planidia were placed on third, fourth, or early-fifth instars (y = 74.84 − 6.25x) or late-fifth instars (y = 52.31 + 7.725x − 1.064x²).

the other fields. Nearly 75% of the parasitized corn earworm larvae were superparasitized. No *A. marmoratus* eclosed from pupae with more than four maggots and nearly 90% of those that eclosed were from hosts with fewer than three maggots (Fig. 6). For hosts yielding adult *A. marmoratus*, the average number of maggots per host was 1.5 ± 0.14 maggots. Parasitized corn earworm that died during the pupal stage averaged more maggots than those that produced adults (4.2 ± 0.39 maggots) and those that did not pupate averaged more maggots than those that died as pupae (7.9 ± 0.87 maggots).

For nonparasitized, field-collected larvae, percentage of larval mortality, pupal mortality, and adult eclosion were similar for feral and F_1 insects (G = 0.986, df = 2, P = 0.611). Too few parasitized, feral insects (10) were collected for a similar statistical comparison. For all field-collected corn earworm, 82% of the nonparasitized pupae eclosed to an adult form compared with 40% for parasitized pupae.

The number of days from time of collection to pupation for field-collected larvae ranged from 3 to 14 d. Of nonparasitized F_1 larvae, 51% pupated within 7 d regardless of whether they subsequently died as pupae or eclosed as adults (G = 2.077, df = 3, P = 0.557). However, for parasitized F_1 larvae, those that died as pupae took longer to reach the pupal stage than those that eclosed as adults (P = 0.005, Fisher exact test). For hosts from which *A. marmoratus* eclosed, the

Table 1. Percentage parasitism and average number of maggots per parasitized corn earworm larva following the release of *A. marmoratus*

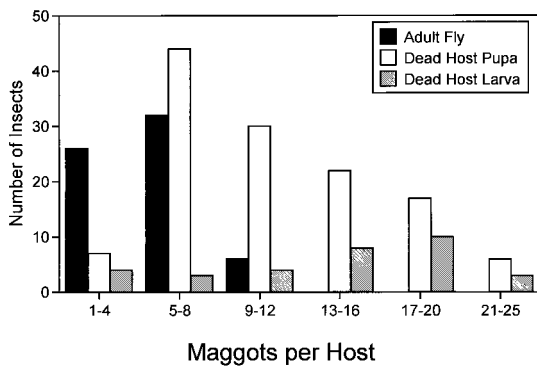| Study field	Size, ha	Release rate, ♀♀/ha	F_1 larvae recovered, %	No. of feral larvae	Parasitism, %	Maggots per parasitized larva
Clyatt	5.7	159	4.4	0	0	0
Griner	6.4	405	30.4	0	37.0	4.4
Harper-1	9.0	276	9.6	4	25.9	6.0
Harper-2	2.4	376	20.0	5	26.4	5.9
Houston	2.7	168	25.8	33	20.0	3.9
Richardson	3.2	721	23.8	12	49.3	5.3
Rowan-1	0.7	549	19.2	0	4.3	2.0
Rowan-2	2.6	150	23.8	0	1.8	4.0
Rowan-3	1.9	506	31.2	0	25.3	4.1
Stone	3.2	591	34.8	39	4.4	1.5

Fig. 6. Percentage of *A. marmoratus* that eclosed, or host mortality as a function of number of maggots per parasitized corn earworm.

number of days to pupation was similar to that of nonparasitized F_1 insects ($G = 5.545$, df $= 4$, $P = 0.236$). Likewise, for nonparasitized insects, a three-way log likelihood ratio test (insect type [feral or F_1] by days to pupation by number of pupae eclosing) was not significant ($G = 6.248$, df $= 4$, $P > 0.1$). This suggests that feral larvae were of the same age as F_1 larvae.

Decline in survivorship of *A. marmoratus* from corn earworm as a function of the number of maggots per host was linear whether larvae were exposed to planidia in the laboratory or field (Fig. 7). However, the y intercept was greater and the regression slope more gradual for larvae exposed to planidia in the laboratory than for field-collected larvae.

There was a significant linear relationship ($F = 179.04$; df $= 1$, 9; $P < 0.0001$) between parasitism rate in the field and the number of maggots per corn earworm larva (Fig. 8). This linear relationship predicts that when the parasitism rate approaches 40%, there
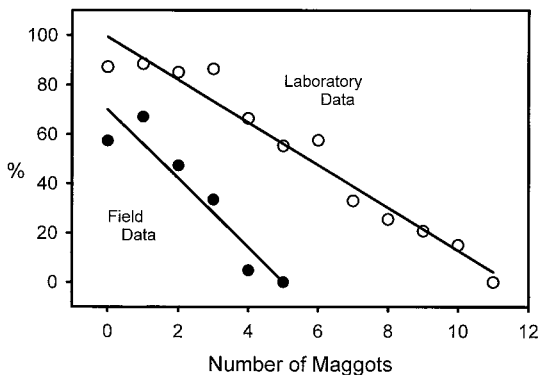
would be two maggots per host. Therefore, from the field survival data in Fig. 7, we would expect *A. marmoratus* to eclose from 50% of the parasitized hosts (two maggots per host) when parasitism approached 40%. At >75% parasitism little eclosion would be expected because the average number of maggots per corn earworm larva is greater than four. The number of females released per hectare did not significantly influence percentage parasitism ($F = 2.09$; df $= 1$, 9; $P = 0.1865$) or average number of maggots per parasitized insect ($F = 1.46$; df $= 1$, 9; $P = 0.262$).

Discussion

Superparasitism by *A. marmoratus* was common whether corn earworm larvae were exposed to planidia in the laboratory or to adult parasitoids in whorl-stage corn. Percentage of hosts with parasitoid eclosion declined linearly with number of maggots per host. The number of maggots that prevented parasitoid eclosion in field studies was less than half the number required in the laboratory. The difference may be caused by greater stress on insects in whorl-stage corn than on larvae in the more uniform rearing conditions of the laboratory. Similarly, Proshold et al. (1998) found no eclosion of parasitoids from field-collected corn earworm larvae with more than four maggots.

In laboratory studies with superparasitized *Heliothis virescens* (F.), Hughes (1975) found that survival of *A. marmoratus* was dependent on the number of parasitoids as well as rearing temperature. Although >20% of the pupae with 10–12 maggots produced an adult parasitoid, no parasitoid eclosed if host pupae had 13 or more maggots. In our studies, a parasitoid eclosed from 13% of the corn earworm pupae with 10 maggots, but none eclosed if the host had >10 maggots.

Hughes (1975) found that *A. marmoratus* successfully parasitizes second-instar *H. virescens* but parasitoid survival is better (48 versus 25%) when fifth-instars are attacked. In the corn earworm, we found that parasitoid survival is higher when fifth instars are parasitized than when earlier instars are parasitized. Similarly, parasitoid survival from parasitized, late-
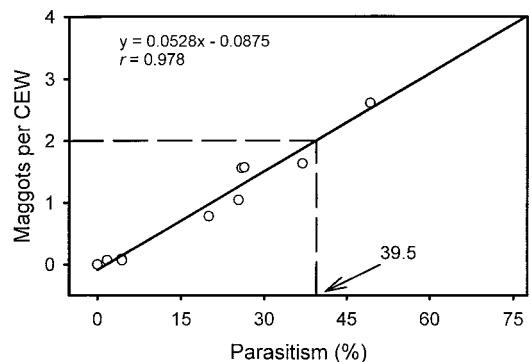

Fig. 7. Percentage eclosion of *A. marmoratus* from corn earworm as a function of the number of maggots per corn earworm larva when *A. marmoratus* females were released in whorl-stage corn ($y = 70.02 - 13.98x$, averaged over fields), and when corn earworm larvae were parasitized in the laboratory ($y = 99.24 - 8.65x$, data from tests 2 through 4 combined).

Fig. 8. Average number of maggots per corn earworm larva as a function of percentage parasitism after the release of *A. marmoratus* females in 10 study fields in 1996.

fifth instars is greater than that of parasitized, early-fifth instars. The greater the number of maggots per host, the lower the likelihood that the host would pupate or yield a parasitoid.

In the field, the number of maggots per corn earworm is highly correlated with percentage parasitism. An average of two maggots per corn earworm is achieved at 40% parasitism. Only half of the hosts with two maggots produce an adult parasitoid. It was calculated that 75% parasitism would yield an average of four maggots per corn earworm, the limit for any survival of *A. marmoratus.* Females produce high numbers of planidia, a characteristic that is beneficial for rearing parasitoids for inundative release, but apparently works against perpetuating high parasitoid populations in subsequent generations. *A. marmoratus* appears to be very efficient in finding host larvae even at low host densities. Proshold et al. (1997) found no correlation in percentage parasitism and distance within 0.8 km of the release site, but they observed a positive correlation between percentage parasitism and host larval density. This efficiency and high fecundity, along with the apparent inability of tachinid females to detect hosts that have previously been parasitized (van Alphen and Visser 1990), may limit the role of *A. marmoratus* in augmentative control. Inundative releases may be most effective against the first generation of corn earworm, for example, to reduce the seasonal increase of corn earworm populations. If the purpose for releasing *A. marmoratus* is to increase parasitism of subsequent generations of corn earworms, these data suggest that release rates will need to be adjusted to host density so that percentage parasitism remains low enough to allow acceptable production of adult parasitoids yet high enough to warrant releases.

Acknowledgments

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